THE LIFE CYCLE OF *CYCLOPS BICUSPIDATUS THOMASI* S. A. FORBES IN LEAVENWORTH COUNTY STATE LAKE, KANSAS, U.S.A. (COPEPODA)

BY

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The copepod *Cyclops bicuspidatus* is a variable species, more like *C. vernalis* Fischer than *C. viridis* (Jurine) (cf. Yeatman, 1944). It is divided into several subspecies; e.g., *C. b. lubbocki* Brady, *C. b. navus* Herrick, *C. b. thomasi* Forbes, and should demonstrate interesting patterns of ecological and physiological adaptation.

A doubtful record of *C. bicuspidatus* Claus was reported from Woods Hole, Massachusetts (Forbes, 1897). Most, if not all reports of *C. bicuspidatus* in North America can be referred to *C. bicuspidatus thomasi* and will be so considered in this paper. *C. b. thomasi, Cyclops vernalis* and *Mesocyclops edax* (S. A. Forbes) are the three most commonly occurring cyclopoids in the limnetic zone of lakes (Pennak, 1957).

In Colorado, *C. b. thomasi* was found at all elevations from 1250 to 3700 m (Dodds, 1919) and collected in every month of the year in seven different mountain lakes (Pennak, 1949). Tash has recently collected all copepodid stages in mid summer in alpine lakes in Oregon. Individuals were found throughout the year in Lewis and Clark Reservoir, South Dakota, but were more abundant during the winter (Tash, Swanson & Siefert, 1966). Specimens were collected throughout the year in Lake Erie, but were rare during the summer (Chandler, 1940).

Most records of *C. b. thomasi* indicate a seasonal distribution with only a few reports of summer populations, such as in Douglas Lake, Michigan (Moore, 1939). The species was present in the deep waters of Lake Erie in June and in shallow waters in spring and autumn (Ewers, 1930) and was collected in Put-in-Bay in western Lake Erie in mid June to mid July 1958 (Davis, 1959). In western Lake Erie in 1946-48, *C. b. thomasi* occurred from December through mid July and disappeared when the temperature of the water reached about 15° C (Andrews, 1953). However, Davis (1959) reported temperatures of about 21° C. Yeatman

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(1956), who collected from Woods Reservoir, Tennessee, concluded that *C. b. thomasi* is a cold water copepod that appears in winter and early spring collections and disappears before mid May. The aestival season is spent as diapausing stage IV copepodids (Yeatman, 1956; Cole, 1953).

C. b. thomasi was first collected in the winter and spring in Kansas (Leonard & Ponder, 1949). Subsequent collections in Nemaha and Leavenworth County State Lakes, Kansas, substantiate Yeatman's conclusions (Tash & Armitage, 1960; Armitage, 1961). However, many of these reports do not indicate how many population cycles occur during the period of activity. This problem becomes especially interesting because the species may be perennial in waters that remain sufficiently cool in summer or seasonal in other bodies of water that become too warm in summer.

METHODS

Collections were made weekly (except for a period in late December and early January) from 28 September 1962 to 24 May 1963 inclusive. Quantitative samples were taken with a #16 net on an uncalibrated Clarke-Bumpus sampler towed diagonally. The sampler was raised slowly from the bottom to the top of the lake while the boat cruised through the limnetic zone. The lake is about 13 m deep at maximum (Armitage, 1962). Temperature of the water was taken at meter intervals with a Whitney underwater thermometer. When ice conditions prevented use of a boat, qualitative samples of plankton were taken with a number 25 net hauled vertically through a hole in the ice. Samples were immediately preserved in 10% formalin. Subsequently, the samples were stored in 80% ethanol.

All copepodid stages in the quantitative samples were enumerated in either three 1 ml aliquots of the sample (in large samples) or in the entire sample (in small samples) and the numbers per liter determined. For this computation, one revolution of the Clarke-Bumpus sampler was equated to 4 liters. The relative abundance of each copepodid stage and the mean number of eggs per female were determined in all samples.

RESULTS

The first individuals of *C. bicuspidatus thomasi* were collected in mid October. Copepodid stages IV and V were present in low numbers (fig. 1). Stage VI, ♂ and ♀, were present in such low numbers that they were not detected in the quantitative counts. However, a careful search through the sample revealed these stages (fig. 2). Hereafter, copepodid stages will be designated by a C plus number of the stage; e.g., CIV for copepodid stage IV.

By early November, there was about one adult per liter. CIV increased to more than 3/1 by mid November. Presumably these CIV individuals resulted from the termination of diapause. The termination of diapause must occur over a period

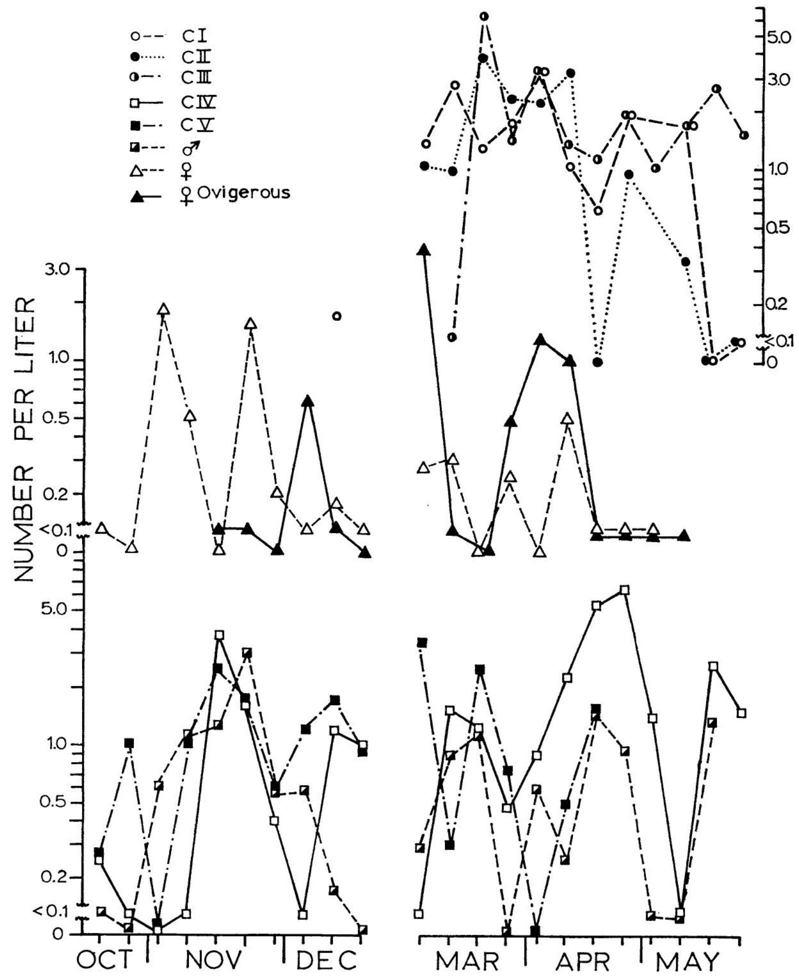

Fig. 1. Quantitative changes in the population cycle of *Cyclops bicuspidatus thomasi* Forbes in Leavenworth County State Lake, Kansas. Lower: CIV, CV, CVI ♂. Middle: CVI ♀, CVI, ovigerous ♀. Upper: CI, CII, CIII. Upper right ordinate is numbers per liter.

of at least 2 months and perhaps for almost 4 months. The decrease of CIV in late October probably resulted from molting to CV as CV increased during this period (fig. 1, 2). The subsequent decrease of CV was paralleled by the appearance of CVI. By mid November a few ovigerous females were present, but did not reach a peak (of 0.6/1) until mid December. Not until late December were a few CI and CIII found. A few CII were found in January. It seems most likely that the peaks of CIV in mid November and mid December resulted from further termination of diapause rather than from reproduction by the ovigerous females.

The factors that terminate diapause are not apparent from the data obtained during these collections. Temperature may be a critical factor. However, CIV first appeared while the average temperature exceeded 15° C (fig. 3). This mean temperature decreased to 3.2° C by mid December. Thus termination of diapause occurred over a wide range of temperatures. However, this period was marked by decreasing temperature. This change of temperature could act as a stimulus to terminate diapause. This period is also one of decreasing photoperiod. Since temperature may vary from year to year and since termination of diapause began before the period of decreasing temperature, photoperiod seems a more likely stimulus. Light induces hatching of resting eggs of *Daphnia* (Pancella & Stross, 1963).

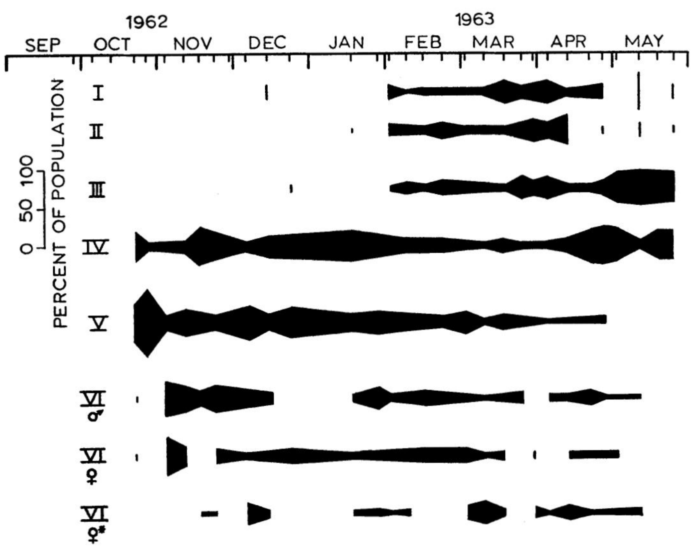

Fig. 2. Seasonal changes in the relative composition of the population of *Cyclops bicuspidatus thomasi* Forbes in Leavenworth County State Lake, Kansas.

Little reproduction occurred before February when all stages were present (fig. 2). The number of eggs per ovigerous female increased from a mean of 28.6 in mid November to a mean of 35 in mid December (fig. 3). Ovigerous females were rare during January and February, but became common again in March. The mean number of eggs per ovigerous female was the same in March as in December. From mid March through mid April there was a gradual increase in the mean number of eggs per ovigerous female to a peak of 42.8. After mid April, the temperature exceeded 15° C and the mean number of eggs per ovigerous female decreased significantly.

The population trend paralleled the trend of egg number. During March and April the total numbers of all stages averaged 10.6/1 with a maximum of 16.3/1 in mid March. This maximum is higher than the maximum of 11/1 (Andrews, 1953) and 7/1 (Chandler, 1940) reported for Lake Erie. The numbers decreased to an average of 4.0/1 in May. By late May only stages III and IV were present in any numbers (figs. 1, 2).

Presumably as individuals molted to CIV, they entered diapause. Such an interpretation is supported by the disappearance of CV in late April. This disappearance indicates that there was no further molting from CIV to CV. The inhibition of molt must be a prerequisite for diapause. Many of the CIII collected in mid May were covered with algae and appeared to be of some age. Whether these individuals diapaused or molted is unknown; the lack of CIII in October is consistent with a failure of CIII to diapause. If the inhibition of molt is general, these CIII may be lost to the population.

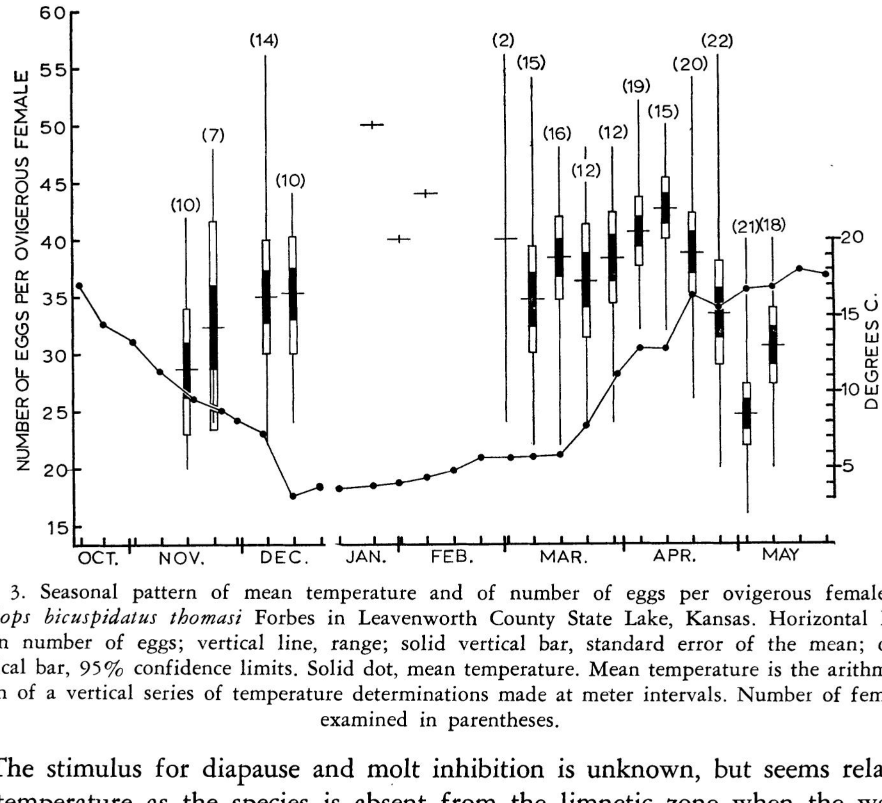

Fig. 3. Seasonal pattern of mean temperature and of number of eggs per ovigerous female of *Cyclops bicuspidatus thomasi* Forbes in Leavenworth County State Lake, Kansas. Horizontal line, mean number of eggs; vertical line, range; solid vertical bar, standard error of the mean; open vertical bar, 95% confidence limits. Solid dot, mean temperature. Mean temperature is the arithmetic mean of a vertical series of temperature determinations made at meter intervals. Number of females examined in parentheses.

The stimulus for diapause and molt inhibition is unknown, but seems related to temperature as the species is absent from the limnetic zone when the water warms. Both reproduction (fig. 3) and total numbers (fig. 1) decreased markedly when the mean temperature exceeded 15° C. The effect of temperature is not abrupt and other factors may be important; e.g., photoperiod, which affects diapause and molting in arthropods (Farner, 1961).

DISCUSSION

One of the interesting questions related to the population cycle is whether the CIV must pass through an obligatory diapause or whether the fate of CIV is labile and directed by the environment. An examination of the number of population cycles during the period of activity should indicate which of the above conditions exists.

The reports from Europe concerning *Cyclops bicuspidatus* Claus indicate that the species may be polycyclic in ponds (Wolf, 1905; Røen, 1957; Gurney, 1933) and may form summer resting stages (Spandl, 1926; Herbst, 1951; Røen, 1957). *C. b. thomasi* is monocyclic in Lake Erie and requires a month or more for development from egg to adult (Andrews, 1953). The species seems to complete two cycles per year in Leavenworth County State Lake. There is essentially no reproduction until February so that all adults must come from CIV that were in diapause. A large number of CI appears in early March. These individuals resulted from the population of ovigerous females which developed during late January and early February. By mid March CIII exceeds 6/1. By early April another peak of ovigerous females develops. The time from one peak of ovigerous females to the next is about 35 days, sufficient time for a complete life cycle. Reproduction by the ovigerous females during April results in a peak of CIV by early May. Presumably most of these CIV diapause and complete their life cycle the following winter. Thus one life cycle is completed in the spring and the second is started in late spring and completed during the winter with diapause occurring during the summer.

The two population cycles are not sharply delimited as early copepodid stages are present in excess of 1/1 for about three months in late winter and spring. In a real sense, there is one long season of reproduction so that the two cycles overlap. The two cycles are distinguished primarily by the two major peaks of CIV, V, and VI. It should also be noted that CIV forms a third peak in late May. This peak could represent either a part of a prolonged second cycle or the beginning of a third cycle. In either event, the two peaks (two cycles?) merge at the CIV stage when the individuals diapause. This common fate of the copepodids is emphasized by the disappearance of CV after mid April. The CVI (♂ and ♀) that were found in May can also be accounted for as part of a broad second cycle.

The interpretation of the reproductive cycle is difficult because nothing is known about the effects of temperature and photoperiod on the rate of development and molting. Theoretically, the increased temperatures in late spring could accelerate or depress metabolism. A study of the physiology of this species and of *Mesocyclops edax* is currently underway at the University of Kansas.

In summary, the life cycle is interpreted to consist of CIV emerging from diapause from October through January. Development produces CV and CVI, but little reproduction occurs before February. The first cycle is completed when ovigerous females develop in mid March. A second cycle develops by late April. Presumably many of the CIV of this cycle diapause and the cycle is completed the following winter. However, either the second cycle has a prolonged period or a small third cycle occurs which merges at CIV with the second cycle and both cycles contribute to the continuation of activity the following winter.

The fact that the species has more than one cycle per season indicates that diapause is not obligatory. The factors that determine diapause are of great interest. The species may be polymorphic or perhaps selection has acted to produce the pattern of summer diapause in some populations (Yeatman, 1956). In this connection, it is worthwhile to examine the relationship between *C. b. thomasi* and *Mesocyclops edax* (S. A. Forbes).

Pennak (1957) emphasized that either of these species or *C. vernalis* is the typical cyclopoid of the limnetic zone. (Note: Pennak refers to *M. leuckarti* (Claus)), but recent evaluations indicate that the limnetic species is *M. edax* (cf. Yeatman, 1959). Cole (1953) suggested that diapause by *C. b. thomasi* may make possible its coexistence in the same water with *M. edax*. When both species exist in the same lake in North America, *M. edax* is abundant in the summer and fall and *C. b. thomasi* is abundant in the winter and spring. The population cycles overlap; e.g., Andrews (1953), and this overlap occurs in Leavenworth Country State Lake.

During this study, *M. edax* was not collected from mid December until mid March. In March and April CIV, CV, and CVI were collected. The appearance of these stages implies that *M. edax* survives the winter as diapausing CIV. Ovigerous females were present in April and overlapped in time with females of *C. b. thomasi*. The total population of *M. edax* averaged 25/1 in May. Thus the period of rapid population increase of *M. edax* coincided with a period of population decline by *C. b. thomasi* (4/1 in May). An earlier study of the summer populations (Tash & Armitage, 1960) revealed the presence of *M. edax*, but not of *C. b. thomasi*.

M. edax and *C. b. thomasi* utilize some of the same energy sources. Many instances were found in the collections in which one or the other or both species had seized CI or CII stages of *Diaptomus pallidus* Herrick, 1879. A nauplius, a CIII *D. pallidus* and a neonata of *Daphnia galeata mendotae* Birge, 1918, were each found once in the jaws of *C. b. thomasi*. These superficial observations indicate that *Diaptomus pallidus* may be the most important prey species of the cyclopoids. *Diaptomus pallidus* is perennial and reproduces throughout the year in Leavenworth County State Lake (Armitage & Tash, 1960; Armitage unpublished data and data from these collections) and would thus be a continuous source of energy. Other sources of energy also may be used by cyclopoids. Although the food habits of *C. b. thomasi* and *M. edax* have not been evaluated, the potential for competition (Milne, 1961) exists.

Diapause in these two species may be a necessary preadaptation that enables them to coexist in the same body of water, but which evolved as an adaptation to unfavorable environmental conditions. *C. bicuspidatus* in Europe frequently occurs in temporary ponds (Wolf, 1905; Hartwig, 1901; Røen, 1957). Obviously a diapausing stage is a prime adaptation for surviving a temporary absence of water. However, in order for the adaptation to be fully effective, the organism must "anticipate" the forthcoming unfavorable conditions. Such "anticipation" requires a "Zeitgeber". Both photoperiod and temperature may function as a "Zeitgeber" (Bunning, 1964). Because *C. bicuspidatus* may be perennial when conditions permit, photoperiod seems an unlikely "Zeitgeber". Temperature seems more likely and its likelihood is supported by the temperature relationships cited previously. Also, as a temperate-zone pond begins to dry up, it also warms up. Thus the increase in temperature could stimulate diapause so that encystment could take place before the water is gone.

The tendency for a polycyclic life cycle is also adaptive. The almost continuous reproduction enables the species to populate and maintain numbers when its environment is favorable. Also, and perhaps more significantly, this life cycle ensures that stages are always present and available for diapause when environmental conditions warrant. For example, CIV was present throughout the period of activity (fig. 2).

The assumption in this discussion is that this species is originally one of temporary pools, the predominant pattern in Europe (Røen, 1957). However, there appears to be no factor in the biology of the species that prevents its occurrence in lakes. In North America, *C. b. thomasi* is commonly limnetic. The adaptation for existence in temporary ponds is easily modified to the pattern described previously. Thus, this species may occupy the limnetic zone during the cool part of the year and not compete with *M. edax* which is present during the warm season. Although this discussion has emphasized the possible interaction between *C. b. thomasi* and *M. edax*, other species patterns may occur. Tash recently collected *C. b. thomasi* during the winter and spring in Upper Klamath Lake, Oregon. However, the summer cyclopoid is *Macrocyclops albidus* (Jurine).

Perhaps the presence of *C. b. thomasi* and some other similar sized cyclopoids in the same lake prevents each species from broadening its ecological tolerance and becoming perennial. The investigation of the physiological ecology of cyclopoid copepods from a wide variety of habitats should illuminate the evolutionary mechanisms that have produced the present patterns of distribution.

ZUSAMMENFASSUNG

Der Populationszyklus von *Cyclops bicuspidatus thomasi* vollzieht sich in Leavenworth County State Lake, Kansas, im Winter und Frühling. Die Reproduktion ist vorwiegend polyzyklisch; es lassen sich jedoch zwei Hauptgipfel — und möglicherweise ein weniger ausgeprägter dritter Gipfel — unterscheiden.

Die Maximalzahlen im März waren 16,2/l; als Durchschnittszahl wurde für März und April 10,6/l und für den Mai 4,0/l ermittelt. Reproduktions- und Gesamtindividuenzahlen verminderten sich merklich, nachdem die durchschnittliche Wassertemperatur über 15° C anstieg.

Adaptive Mechanismen, welche *C. b. thomasi* an die Koexistenz mit *Mesocyclops edax* oder andere große Cyclopoiden in Seen präadaptieren, werden diskutiert.

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